



Waterbird assemblages of Australia's largest east-coast wetland complex: environmental determinants of spatial and temporal distribution

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ABSTRACT

Context. The extensive Burdekin–Townsville seasonal freshwater wetlands in the Queensland tropics (adjacent to an intertidal Ramsar site) support important waterbird assemblages within and downstream of the Burdekin–Haughton irrigation area. Little evidence is available of the environmental drivers of these assemblages, possibly including the extensive development of irrigated agriculture. **Aims.** We described the composition and dynamics of freshwater waterbird assemblages to identify their environmental determinants and underpin conservation management. **Methods.** We used up to four decades' worth of records of waterbird assemblages, and collected biophysical data from 57 sites and water quality data for 32 sites. We predicted that these measured variables would determine assemblage composition, thereby elucidating the environmental drivers of the assemblages. **Key results.** In total, 100 waterbird and shorebird species were recorded. Individual samples were strongly nested. Species richness increased with area but density decreased. Richness had a humped relationship with water depth. Linear modelling identified mostly weak relationships between species, assemblages and environmental variables (e.g. nutrients). Abundances mostly increased during the dry season but irrigation tailwater reduced seasonal variation in some wetlands. No apparent change in common species' assemblages was evident over four decades. **Conclusions.** The wetlands provide extensive, diverse habitats for rich waterbird assemblages, despite impacts of agricultural development. Impacts on waterbirds appear to be buffered by the extent and complexity of the wetland mosaic that includes modified wetlands. **Implications.** Holistic, active management is required to ensure the long-term conservation of habitats for waterbirds and other biota in the Burdekin–Townsville seasonal freshwater wetlands. Inclusion of these freshwater wetlands in the Ramsar site would be beneficial.

Keywords: agricultural impacts, environmental drivers, floodplain wetlands, management, temporal change, tropics, waterbirds, water quality.

Introduction

Globally, freshwater ecosystems have high biodiversity relative to size but are disproportionately threatened by human activity (Tickner *et al.* 2020) that results in extensive losses of wetland area (Davidson 2014; Fluet-Chouinard *et al.* 2023) and climate change (Grieger *et al.* 2021; Osland *et al.* 2022). Ecosystem services that wetlands provide are important and highly valued (Whiteoak and Binney 2012; de Groot *et al.* 2018; Pearson *et al.* 2021), especially in coastal wetlands (Davidson *et al.* 2019), but suffer from limited information on environmental drivers of community structure and function. Although Australia is the driest inhabited continent, the country has extensive coastal wetlands that are subject to a variety of environmental pressures (Bino *et al.* 2016; Grieger *et al.* 2021). Laurance *et al.* (2011) included coastal floodplains and wetlands as one of the '10 Australian ecosystems most vulnerable to tipping points', partly because of the restricted and fragmented nature of these ecosystems but also environmental constraints and proximity to areas in which land-use change is implemented. Threats include sea-level rise, plant invasion, hydrological change, habitat loss, pollution and altered fire regimes.

Wetlands may be clustered, patchy or dispersed habitats varying greatly in size and permanence. Areas of intensive land development are typically located on coastal floodplains, making the associated wetlands particularly vulnerable to land-use impacts owing to a combination of upstream (development) and downstream (rising sea level) pressures (Bernhardt 2022). For example, in the Great Barrier Reef catchment in north-eastern Queensland, impacts on wetlands accrue from agriculture, infrastructure and water management, especially through changes in hydrological processes, habitat loss, water-quality deterioration and weed invasion (GBRMPA 2013; Davis *et al.* 2014; Adame *et al.* 2019; Pearson *et al.* 2019), although there is little direct evidence concerning waterbirds. Wetlands are an important focus of catchment management because of the role these ecosystems play in local hydrological processes, connectivity to downstream environments, ecosystem services and biodiversity, and appropriate management is required to sustain these values (Adame *et al.* 2019).

Waterbirds are distinct components of the high levels of biodiversity that wetlands support, such that they have been used to provide a globally applicable indication of wetland condition in Australia (Kingsford 1999), Argentina (Sica *et al.* 2020) and the United States (Stevens and Conway 2020), for example. Australia's waterbirds can be highly nomadic, reflecting the variability of the climate, and exploit wetlands as these become available (Halse *et al.* 2005; Kingsford *et al.* 2010), although groundwater-fed coastal wetlands may provide longer-duration or permanent habitat. All wetlands may be threatened by loss of habitat as a result of developments of water resources, flood mitigation and irrigation (Davis *et al.* 2014; Tibby *et al.* 2019; Caley *et al.* 2022). There is a need to understand the values of wetlands and factors that determine condition to guide practical management strategies (Grieger *et al.* 2021).

We assembled data from a series of studies of waterbird assemblages in the coastal floodplain wetlands of the Burdekin River and associated drainages. This floodplain system and the contiguous irrigation area are the largest on the Australian east coast (GBRMPA 2013; Davis *et al.* 2014). The floodplain abuts the intertidal Bowling Green Bay Ramsar wetlands and other wetlands of national importance that are listed in the National Directory of Important Wetlands (DIWA) (Australian Government 2024). We aimed to determine the major drivers of waterbird assemblages and any change in these due to agricultural development on the floodplain, especially from expansion of the irrigation area following the 1987 completion of the Burdekin Falls dam. The dam supplies irrigation water via artificial and natural channels, leading to tailwater supply to drains, natural channels and wetlands. Changes in hydrological processes, extensive land clearing and agricultural expansion have led to enhanced concentrations of nutrients and sediments, and have facilitated weed invasion and other impacts (GBRMPA 2013; Davis *et al.* 2014).

We used data derived from two studies of multiple sites in the 1990s and early 2000s, broad-scale records from the

1990s to 2021, and regular surveys of two important sites between 2012 and 2021. We aimed to identify major factors affecting waterbird assemblages in this complex wetland environment to underpin conservation management planning and activity. Specifically, we hypothesised that:

1. waterbird assemblages are generally similar among the wetlands surveyed;
2. waterbird assemblages vary spatially with wetland character, as defined by 32 measured variables encompassing the timing of sampling (year, month and season), wetland dimensions, hydrological processes, agricultural or urban disturbance, weed growth and water quality (e.g. Ma *et al.* 2010);
3. abundance of waterbird populations and assemblage composition vary seasonally, with maxima in the wet season (Kingsford *et al.* 2010);
4. assemblages vary annually according to antecedent rainfall (Kingsford *et al.* 2010; Kingsford 2013; Caley *et al.* 2022); and
5. assemblages have changed over several decades as a result of floodplain development for agriculture (clearing, levelling, irrigation supply and drainage) (Davis *et al.* 2014).

Methods

We focused on the waterbird assemblages (Anseriformes, Podicipiformes, Gruiformes, Pelecaniformes and Charadriiformes) of the Burdekin–Townsville wetlands (Fig. 1, Supplementary material Table S1). Common and scientific names are provided in Table 1 (more common species) and Table S2 (all species); otherwise, we only use common names. We also refer to the Charadriiformes as shorebirds, following convention (e.g. Driscoll *et al.* 2012).

Sampling area and sites

The climate of the study area is seasonal tropical, with mean minimum and maximum temperatures at Ayr (Fig. 1) of 21.9°C (June) and 35.3°C (February) respectively (Australian Bureau of Meteorology data, 1952–2022). Rainfall is also seasonal, with a summer wet season (here defined as January to April), spring dry season (September to December) and a transitional period overlapping the wet and dry seasons during the period of decline in freshwater flows (May to August) (Fig. S1). Annual rainfall in Ayr (mean 1887–2022, 1056 mm) is highly variable (e.g. during the study period, 366 mm in 1991 and 1363 mm in 2021).

The study was located in the 'Burdekin–Townsville Coastal Aggregation' (Queensland Government 2024), and on the floodplain of the Burdekin–Haughton Water Supply System (BHWSS) and irrigation scheme. This area covers ~1140 km², including 93 km² of freshwater wetlands. The aggregation extends from Ayr north-eastwards to the coast and north-westwards

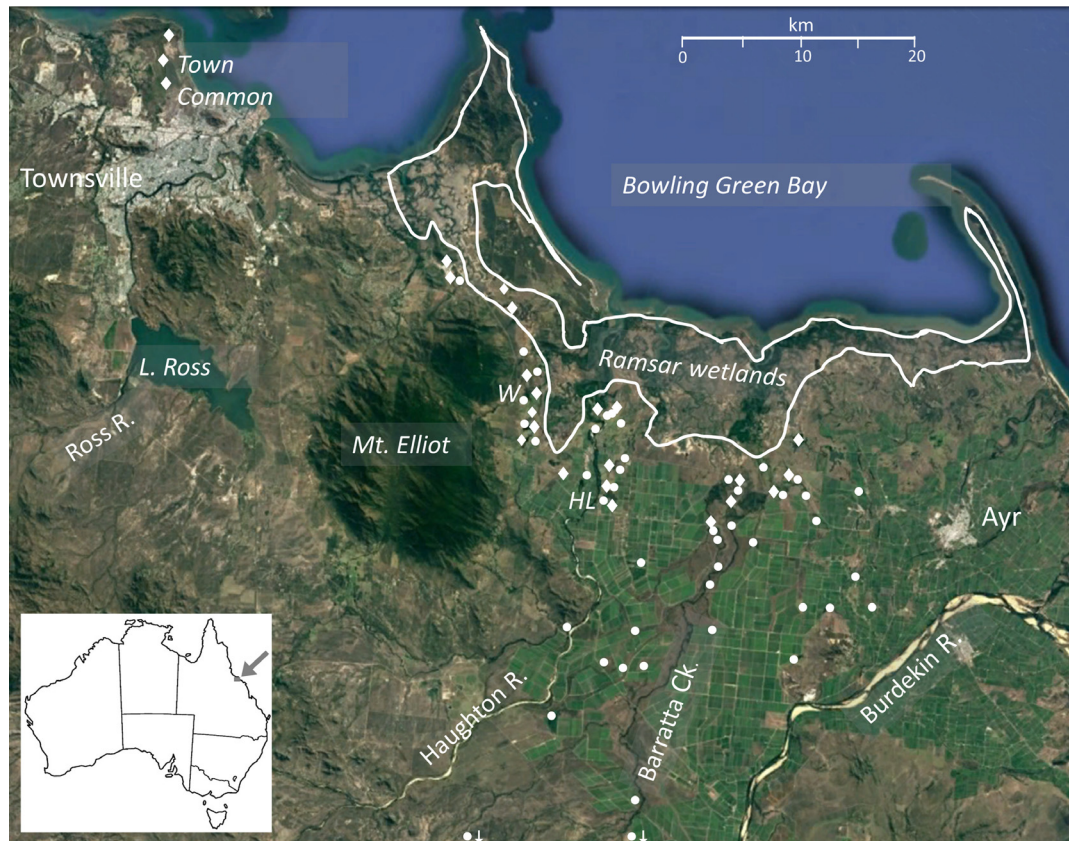


Fig. 1. Google Earth® image of the Burdekin–Townsville study area indicating the locations of sampling sites (Survey 1, white dots; Survey 2, white diamonds), Ramsar tidal wetlands, main towns and rivers, and other points of interest. Sugarcane is coloured mid-green. Forest is dark green and grassland/woodland is pale green or brown. Inset shows location in north-eastern Queensland (approximately 19.5°S, 147.2°E). W, Wongaloo; HL, Horseshoe Lagoon.

to Townsville and includes the Burdekin–Haughton irrigation area (800 km²) which, despite wetland losses, still includes many wetlands. This area also includes the mostly intertidal Bowling Green Bay Ramsar wetlands (GBRMPA 2013), which were excluded from our study (Fig. 1). This complex represents one of the largest concentrations of high-value freshwater, estuarine and marine wetlands in Australia (Davis *et al.* 2014; NQ Dry Tropics 2016).

The floodplain is fed naturally by shallow aquifers, local rainfall and runoff, and overbank flows of the Burdekin River (rarely; Alexander *et al.* 1999) and Haughton River, resulting in the formation of numerous seasonal swamps and shallow lakes, deep perennial riverine lagoons and extensive coastal sedgeland (Fig. S1) (Tait and Veitch 2007; GBRMPA 2013; Queensland Government 2024). The water table is close to ground level on a large proportion of the floodplain. Patches of woodland characterised by *Melaleuca*, *Pandanus* and *Livistona* species occur on raised ground and, along the natural drainage channels, species-rich gallery forest or mangrove forest is prevalent, except where channels have been cleared or burned. The wetlands are of significant conservation value, providing habitat for diverse plant, invertebrate and fish assemblages (Connolly *et al.* 2012; Pearson *et al.* 2019), and

many bird species, some of which occur in nationally significant numbers (Driscoll *et al.* 2012) or are variously threatened (e.g. 17 species of shore or wetland species (Table S2; Garnett and Baker 2021)).

Agricultural development on the floodplain historically depended on rainfall and water derived from wetlands and groundwater (from the 1870s), and subsequently directly from the Burdekin River. The Burdekin Falls dam was completed in 1987 and currently supplies both the subsequently developed irrigation area and groundwater recharge. Downstream of the dam, water is delivered via the river, from which it is pumped into irrigation channels and the Haughton River, and distributed as required to crops and to recharge pits on the lower floodplain. Irrigation runoff enters drains and eventually natural waterways, thereby boosting groundwater levels and providing water to many wetlands during the dry season (Queensland Government 2018). The dam facilitated growth of the irrigation area by ~40,000 ha to a total of 80,000 ha, providing ~25% of Australia's sugar crop (Fig. S2) (GBRMPA 2013). The dam overflows during most years but this does not affect the frequency of rare overbank flooding to the floodplain of the BHWSS (Alexander *et al.* 1999; Cooper *et al.* 2016; Queensland Government 2018).

Table 1. Proportional occurrence frequency (% of all samples in each survey) of the most common waterbird species (Anseriformes, Podicepiformes, Gruiformes, Pelecaniformes and Charadriiformes) in surveys of the study area (36 species representing >0.1% of the total bird count in surveys S1 and S2) and mean mass in surveys S1 and S2 (kg/ha) (sorted by mass; see text); and total richness.

		Surveys and no. of samples (times × sites)							Diet
		BDATA (4235)	WONG (234)	HL (26)	UNSW (121)	DRISC (4)	S1 and 2 (198)	S1 and 2 Mass	
Magpie Goose	<i>Anseranas semipalmata</i>	43.7	44.2	42.3	38.3	48.6	33.9	4193	SFC ^A
Pacific Black Duck	<i>Anas superciliosa</i>	9.30	9.85	2.25	6.61	14.2	14.0	758	SFA
Plumed Whistling-Duck	<i>Dendrocygna eytoni</i>	0.07	0	0	32.2	1.18	18.6	697	SFA ^A
Hardhead	<i>Aythya australis</i>	2.51	2.94	36.5	0.81	2.82	8.48	377	SFA
Yellow-billed Spoonbill	<i>Platalea flavipes</i>	0.24	0.27	0	0.12	0.05	3.04	291	A
Brolga	<i>Antigone rubicunda</i>	2.78	1.35	0.01	1.32	0.43	0.74	237	SFCTA
Royal Spoonbill	<i>Platalea regia</i>	1.08	1.11	0.13	0.50	2.65	2.52	223	A
Australian Pelican	<i>Pelecanus conspicillatus</i>	1.27	1.35	1.35	0.62	0.38	0.65	178	TA
Australian White Ibis	<i>Threskiornis moluccus</i>	0.36	0.38	0.06	0.27	0.18	1.65	153	TA
Straw-necked Ibis	<i>Threskiornis spinicollis</i>	0.74	0.85	0.01	0.09	0.02	2.00	138	T
Black Swan	<i>Cygnus atratus</i>	9.51	10.6	5.12	6.71	5.18	0.31	91	F
Little Black Cormorant	<i>Phalacrocorax sulcirostris</i>	0.31	0.30	1.41	0.11	1.99	1.27	56	A
Great Egret	<i>Ardea alba</i>	0.59	0.56	0.13	0.11	1.83	0.71	34	TA
Black-winged Stilt	<i>Himantopus leucocephalus</i>	3.80	3.94	0.04	0.19	2.18	3.54	32	A
Masked Lapwing	<i>Vanellus miles</i>	0.70	0.72	0.33	0.33	0.90	1.91	31	TA
Australasian Darter	<i>Anhinga novaehollandiae</i>	0.05	0.06	1.29	0.04	0.47	0.33	26	A
Pied Cormorant	<i>Phalacrocorax varius</i>	0.01	0.02	0.15	0.07	0.01	0.01	20	A
Grey Teal	<i>Anas gracilis</i>	18.4	17.6	0.43	4.38	0.88	0.65	16	SK
Australian Pelican	<i>Pelecanus conspicillatus</i>	1.27	1.35	1.35	0.62	0.38	0.65	16	TA
Australasian Grebe	<i>Tachybaptus novaehollandiae</i>	0.09	0.10	1.67	0	1.34	1.55	15	A
White-faced Heron	<i>Egretta novaehollandiae</i>	0.12	0.09	0.02	0.20	0.15	0.51	15	TA
Black-necked Stork	<i>Ephippiorhynchus asiaticus</i>	0.08	0.09	0.03	0.02	0.07	0.05	7	A
Whiskered Tern	<i>Chlidonias hybrida</i>	0.23	0.21	2.87	0.31	1.92	1.32	6	TA
Intermediate Egret	<i>Ardea intermedia</i>	0.57	0.31	0.09	0	3.30	0.28	6	TA
Little Pied Cormorant	<i>Microcarbo melanoleucos</i>	0.09	0.10	0.34	0.01	0.33	0.16	6	A
Black-fronted Dotterel	<i>Elsayornis melanops</i>	0.07	0.08	0.01	0	0.06	0.96	2	TA
Comb-crested Jacana	<i>Irediparra gallinacea</i>	0.08	0.06	0.77	0	0.77	0.09	1.1	STA
Glossy Ibis	<i>Plegadis falcinellus</i>	0.42	0.36	0.02	0.10	0.19	0.04	1.1	SA
Little Egret	<i>Egretta garzetta</i>	0.19	0.20	0.02	0	0.29	0.04	0.7	TA
Cattle Egret	<i>Bubulcus ibis</i>	0.88	0.79	0.13	0	0.67	0.04	0.6	T
Wandering Whistling-Duck	<i>Dendrocygna arcuata</i>	0.36	0.04	0.02	6.23	3.75	0.04	0.5	SF ^A
Cotton Pygmy-goose	<i>Nettapus coromandelianus</i>	0	0	0.48	0	0.35	<0.1	<0.5	SFA
Eurasian Coot	<i>Fulica atra</i>	0	0	1.98	0	0	<0.1	<0.5	F
Great Cormorant	<i>Phalacrocorax carbo</i>	0	0	0.04	0	0	<0.1	<0.5	A
Red-capped Plover	<i>Charadrius ruficapillus</i>	0.04	0.05	0	0	0	<0.1	<0.5	A
White-necked Heron	<i>Ardea pacifica</i>	0.29	0.32	0.01	0	0.14	<0.1	<0.5	TA
Total richness (number of species on database (Table S2))		100	61	40	30	43	47		

Surveys include: BirdLife Australia (2022) (BDATA), Wongaloo (WONG) and Horseshoe Lagoon (HL); University of New South Wales (UNSW); Driscoll *et al.* (2012) (DRISC); and this study (Surveys 1 and 2). Numbers of samples (in parentheses) include times and sites. See Table S2 for full species list. Diet summary from Garnett *et al.* (2015): S, seeds; F, foliage; C, corms and tubers; T and A, respectively, terrestrial and aquatic invertebrates and vertebrates.

^AIncluding terrestrial grazing.

Development of the irrigation area for sugarcane production involved clearing of vegetation, filling of shallow wetlands, levelling of land and establishment of irrigation infrastructure. According to GBRMPA (2013), this has led to as much as 57% loss of original lacustrine wetlands and 40% loss of palustrine wetlands. Conversely, extensive development of irrigation channels and drains (387 km of channels and 366 km of drains; Sunwater 2024), weirs, balancing storages and ponded pastures has maintained the total area of wetlands at ~106% of the pre-clearance area. There were 3.8× and 1.8× increases in the areas of highly modified lacustrine and palustrine wetlands since pre-clearing of farmland respectively (Queensland Government 2024) (Table S3).

Impacts or threats to wetlands (Table S4) include changes to hydrological processes, with potentially positive or negative effects on waterbirds depending on the associated reliance on seasonal or permanent wetlands; changes to water quality that may increase productivity but deleteriously alter aquatic assemblages; loss of riparian vegetation that provides nesting or roosting sites; establishment of invasive weeds, including water hyacinth (*Eichhornia crassipes*), para grass (*Urochloa mutica*) and hymenachne (*Hymenachne amplexicaulis*) (the latter two species having been introduced to ponded pastures) that may choke waterways and impede reaeration (reducing dissolved oxygen saturation), thereby precluding access by many fish species; and damage by feral pigs, *Sus scrofa* (Connolly *et al.* 2012; Perna *et al.* 2012; GBRMPA 2013; Davis *et al.* 2014; NQ Dry Tropics 2016; Waltham *et al.* 2020).

In our surveys, freshwater wetland sites were located (i) upstream of the Ramsar site and within the BHWSS, including (ii) along Barratta Creek and (iii) Horseshoe Lagoon Conservation Park (0.8 km²); (iv) at Wongaloo Conservation Park (18 km²), adjacent to the BHWSS; and (v) at the Townsville Town Common conservation area (40 km²) (Tait and Veitch 2007) (Fig. 1). The Wongaloo and Townsville Town Common wetlands comprise mainly seasonal vegetated and open-water swamps but do not receive irrigation drainage and have no sugarcane growing in the catchments. Wongaloo is subject to partial cattle grazing. Horseshoe Lagoon is an open-water habitat situated within the agricultural area and artificially perennial because it receives irrigation tailwater.

Data collection

We use the terms ‘survey’ to describe an organised series of samples (or datasets) and ‘sample’ to describe a single census or count at a single site and time. Datasets from seven surveys and several univariate and multivariate analyses were used in this study to address the five hypotheses (Table S5) as described below.

We undertook two separate surveys: (1) comprising two dry-season and two wet-season sets of samples from each of 32 sites in 1991–1993; and (2) comprising three samples from each of 25 sites in June, July and August 2003. Sampling sites

were selected from an initial listing of over 400 individual wetlands according to representativeness and accessibility, from upstream to downstream and east to west on the floodplain (Fig. 1; Table S1). These ranged from 0.1 to 400 ha in area and included only discrete, freshwater/slightly brackish waterbodies such as riverine lagoons and extensive swamps. Identification and counts of waterbirds were made using binoculars and telescope from vantage points around entire wetlands or around defined portions of more extensive waterbodies. Counts were expressed as absolute numbers per sample and as density (numbers of waterbirds per ha sampled). Density and presence/absence data were used for most analyses.

We also accessed other datasets from (3) the Birddata Atlas database (BirdLife Australia 2022) for the whole study area for 1972–2021, for 2012–2021 at (4) Wongaloo and (5) Horseshoe Lagoon (Fig. 1), during which multiple surveys were undertaken each year; (6) an aerial survey by the University of New South Wales (Kingsford and Porter 2009; Kingsford *et al.* 2020); and (7) sites ground-truthed during an aerial survey by Driscoll *et al.* (2012). Breeding activity (presence of accompanied juvenile birds) was noted during surveys of Wongaloo but was not otherwise consistently recorded. The abundance of cryptic species, especially crakes and rails (Gruiformes: Rallidae) was likely underestimated in all these surveys and occurrence of rarer species may have been missed because of limitations in numbers of sampling sites and times.

In Surveys 1 and 2, we recorded up to 32 environmental variables for each sample as potential influences on waterbird assemblages (Table S6). We recorded, for each sample (site and time), the area surveyed; estimated maximum water depth; riparian native tree diversity (number of species along ~50 m of representative wetland perimeter) as a measure of condition; whether the wetland dried during the study period; distance of the wetland from the coast and agricultural influences (using Google Earth for the year sampled) as possible proxies for agricultural or saline disturbance; species richness of aquatic plants at access points; antecedent annual rainfall at Ayr; and antecedent discharge for Barratta Creek. Additionally, for each sample in Survey 1, we further characterised each site by measuring a standard suite of water quality variables *in situ* (temperature, conductivity, pH and dissolved oxygen (using Yellow Springs Instruments meters) and collected water samples from 20 to 30 cm below the water surface directly into sample bottles and preserved these for subsequent analysis. Bottles were selected in accordance with requirements for preservation specified by Australian Standard 2301.1. Samples for nutrient analyses were filtered using Sartorius 0.45-µm cellulose acetate filters, stored in gamma-sterilised plastic tubes and snap-frozen upon arrival at the laboratory (a commercial water analysis laboratory in the Australian Centre for Tropical Freshwater Research (currently TropWater) at James Cook University). Preservation procedures and analysis followed standard methods (APHA 2017).

Variables measured included concentrations of calcium, chlorophyll *a*, potassium, magnesium, sodium, ammonium, nitrate plus nitrite, phosphate, total nitrogen, total phosphorus and total suspended solids. Water quality may not directly affect waterbirds but has a strong bearing on habitat quality and productivity for food organisms (plants, invertebrates and fish), and may therefore be of indirect influence. We were particularly interested in any effects on productivity through nutrient input (positive) and suspended sediments (negative), and indicators of saline conditions (suggesting coastal encroachment). Low levels of dissolved oxygen could indicate limitations on bird food organisms (fish and invertebrates). Other measures formed part of a normal water quality scan that typically accompanies most studies of aquatic ecology.

Statistical analysis

Species counts and densities were $\log_{10}(x + 1)$ transformed to normalise data for analysis, except for some graphical display of abundance. Our analyses included only samples from wetlands that had not dried unless otherwise indicated. Surveys and the analyses applied to the data are listed in Table S5.

We compared assemblage composition among the data sources using Pearson correlation analysis to check for overall agreement. Initial observations suggested that many wetland species select a broad range wetland habitats, such that we predicted that assemblages would be nested subsets of the species pool rather than substantially different – that is, assemblage composition at species-poor sites would be a subset of those at species-rich sites (Patterson and Atmar 1986), forming part of a large metacommunity along a habitat gradient (essentially, wetland size). The degree of nestedness in Surveys 1 and 2 was compared with a null model to determine whether the samples formed a nested hierarchy or were random (Joppa *et al.* 2010) by calculating the ‘nestedness metric based on overlap and decreasing fill’ (NODF) metric and associated statistics (Almeida-Neto and Ulrich 2011), using the online software at <http://ecosoft.alwaysdata.net/>.

Overall waterbird abundance, density and species richness in Surveys 1 and 2 were compared with area, depth and riparian condition using linear regression in SigmaPlot 12.5 (Systat Software, Inc., San Jose, CA, USA). We described broad trophic relationships by grouping species into functional groups determined by the predominant diet (vegetation, including seeds, tubers, etc.; invertebrates; and fish) (Barker and Vestjens 1989; Garnett *et al.* 2015) to provide an outline of major trophic dependencies. Biomass of individual species and functional groups was calculated as mean density $\times$ mean individual mass (from Garnett *et al.* 2015) for Surveys 1 and 2.

We used the Primer package (Primer ver. 7.0.23 and Permanova+ from Quest Research Limited, Massey University, Auckland, New Zealand) for multivariate analysis. We investigated the influence of normalised environmental variables on the bird assemblages in Survey 1 with distance-based linear modelling (DistLM), using the Bray–Curtis

similarity measure on proportional data, given the variation in data sources. DistLM is essentially a multiple regression procedure that uses a similarity matrix of sites based on species’ densities. This seeks the most significant relationships between assemblages and environmental variables by progressively modelling the matrix against the most influential variable, taking the residuals of that relationship, modelling the next most influential variable etc. thereby taking into account correlations between variables (Anderson *et al.* 2008). Thirty-two environmental variables were associated with each sample (Table S6), all of which could affect bird assemblages directly or indirectly. We used multiple regression analysis in Statistix (ver. 10, Analytical Software, Tallahassee, FL, USA) to investigate the influence of the environmental variables on individual species’ densities, total density and species richness.

We included the season, month and year of the variables in the DistLM and multiple regression analyses of Survey 1 data for analysis of short- to medium-term temporal change. We used Atlas count records to identify monthly changes over a full year graphically and via repeated measures ANOVA between seasons for the aggregated data over 7 years (2015–2021) of mean total density, mean total number of species and mean abundance of more common species, using Statistix for the Wongaloo and Horseshoe Lagoon sites. We assigned three nominal seasons, based on rainfall and hydrological characteristics: Wet, Transitional and Dry, representing January–April, May–August and September–December respectively. We similarly analysed changes in the three broad functional (diet) groups. We described short-term temporal changes in abundance during wetland drying graphically for Survey 2 (transitional period only). We also examined the effects of drying on behavioural groupings (foraging methods including aerial, swimming/diving and wading) of the waterbirds that essentially relate to the depth of the water body and associated decline.

We illustrated long-term (decadal) change in assemblages using nonmetric multi-dimension scaling (NMDS) in Primer. We ordinated the annual mean proportional composition of assemblages over three decades for the five surveys that had suitable data (Table S5). We ordinated change in presence/absence data over four decades for all datasets. The effects of time, antecedent rainfall and flow on the proportional data were tested using DistLM. Antecedent rainfall and flow were represented by total annual rainfall at Ayr and discharge in Barratta Creek for the current and previous years to provide an indication of wet and dry years that may influence assemblages. Data were sourced from the Australian Bureau of Meteorology and Queensland Government Water Monitoring Portal (<https://water-monitoring.information.qld.gov.au/>) station 119101A (West Barratta Creek) respectively. Differences between *a priori* groups of samples were investigated using Analysis of Similarities (ANOSIM) in Primer.

Results

Hypothesis 1. Waterbird assemblages are generally similar among the wetlands surveyed

Across all datasets, 100 waterbird (including shorebird) species were recorded (Table S2), of which 44 species occurred in five or more of the datasets. Twenty-six of the remaining species were shorebirds that inhabited the intertidal zone in Australia that was not included in this study. Forty-seven species were recorded during Surveys 1 and 2 (Table 1). There were surprisingly strong correlations among the datasets that recorded abundance, given the different approaches used: for all comparisons, $r \geq 0.7$, except Horseshoe Lagoon, for which $r = 0.55$; in all cases, $P < 0.001$. Nevertheless, individual datasets recorded differences in assemblages: for example, Horseshoe Lagoon and Wongaloo showed strong similarities in common species such as Pacific Black Duck and Black Swan but large differences between cormorants and Hardhead, probably due to the consistently deeper habitat in the former as a result of irrigation drainage.

In Surveys 1 and 2, 24 species occurred in more than 10% of samples, with 12 of these occurring in at least 25% of the samples (Table 1). The most frequently recorded species (among times and sites) were Masked Lapwing, Pacific Black Duck, Australasian Darter and Great Egret, while the most numerically abundant species were Magpie Goose, Pacific Black Duck and Plumed Whistling-Duck. Biomass of individual species followed a similar pattern to that of abundance, with the goose and two duck species predominant. Collective mean biomass of functional groups was estimated at 5992 kg.ha⁻¹, 1249 kg.ha⁻¹ and 370 kg.ha⁻¹ respectively for vegetation, invertebrate and fish consumers.

Nestedness analysis showed that samples from Surveys 1 and 2 were highly nested (NODF index = 67.4, Z-score = 18.85, relative nestedness = 0.43, $P < 0.0001$), indicating that all samples were nested within the entire metacommunity, with no separate groupings.

Hypothesis 2. Wetland bird assemblages vary spatially with wetland character

Abundance of waterbirds increased with wetland area but density decreased (Fig. 2a, b). Species richness increased with abundance and consequently with area (Fig. 2c). Richness increased with maximum depth to a peak at ~3.0 m, after which it declined (Fig. 2d). Richness declined with higher riparian diversity, although the relationship was weak (Fig. 2e). Reflecting the overall data, density of functional groups was negatively correlated with wetland size ($r = -0.414$, -0.420 , -0.366 respectively for vegetation, invertebrate and fish consumers with $P < 0.01$ in each case). However, there were no clear relationships with depth, riparian condition or macrophyte diversity ($r < 0.20$, $P > 0.05$).

Multiple regressions of densities of common species in Survey 1 tested models with temporal, locational, site and

water-quality characteristics. Models with $r^2 > 0.25$ and $P < 0.05$ (Table 2) included those for total density, species richness and density of 15 individual species. Total density was negatively related to sodium (Na) concentration. Species richness showed positive relationships with wetland area and phosphate concentration. All 15 individual species had significant relationships with water-quality variables, with some indicators of productivity being particularly evident (chlorophyll *a* and the nutrients ammonium (NH₄) and phosphate (PO₄), with four, eight and four positive instances respectively) (Table S3). Na (four instances) was negative whereas distance from the coast (two instances) was positive. Other variables, with three or fewer instances, differed among species as to whether these were positive or negative influences. Several variables had no significant relationship. These included most of the direct seasonal indicators, although temperature, drying and instantaneous discharge had minor influence (together, five instances). Correlation analysis between seasonal and water-quality variables yielded none with $r^2 > 0.08$.

DistLM was likewise applied to Survey 1 bird assemblage data and environmental variables, producing a model that included all 32 variables that together explained 46.8% of the variation ($r^2 = 0.468$), although for no individual variable was r^2 greater than 0.060 (Table 3).

Hypothesis 3. Abundance of waterbird populations and assemblage composition vary seasonally, with maxima in the wet season

At Wongaloo, overall abundance, abundance of functional groups, and abundance and percent frequency of occurrence of many common species varied between seasons, particularly with increases in the dry season (Figs 3, S3 and S4; Table S7). The seasonal pattern was not clear at Horseshoe Lagoon, except that the Black Swan appeared to be more abundant in the drier part of the year. At Wongaloo, individual species showed varied patterns of occurrence frequency, with many species present in all months, some more prevalent in the dry season and a few migratory waders such as the Marsh Sandpiper being recorded more frequently in the summer wet season (Fig. S3). In Survey 2, patterns of occurrence frequency across three sites that dried over the 3-month period showed the expected gradual loss of species, with deepwater species leaving first, followed by waders (Table S8). Notably, Brolga remained during drying, feeding on sedge tubers. Evidence of breeding of different species at Wongaloo suggested that breeding occurred mainly during the transitional period and into the dry season (Table S9).

Hypotheses 4 and 5. Assemblages vary annually according to antecedent rainfall and assemblages have changed over several decades

In DistLM, for proportional (density) data, no relationship was evident for assemblages across years (Pseudo- $F = 1.975$,

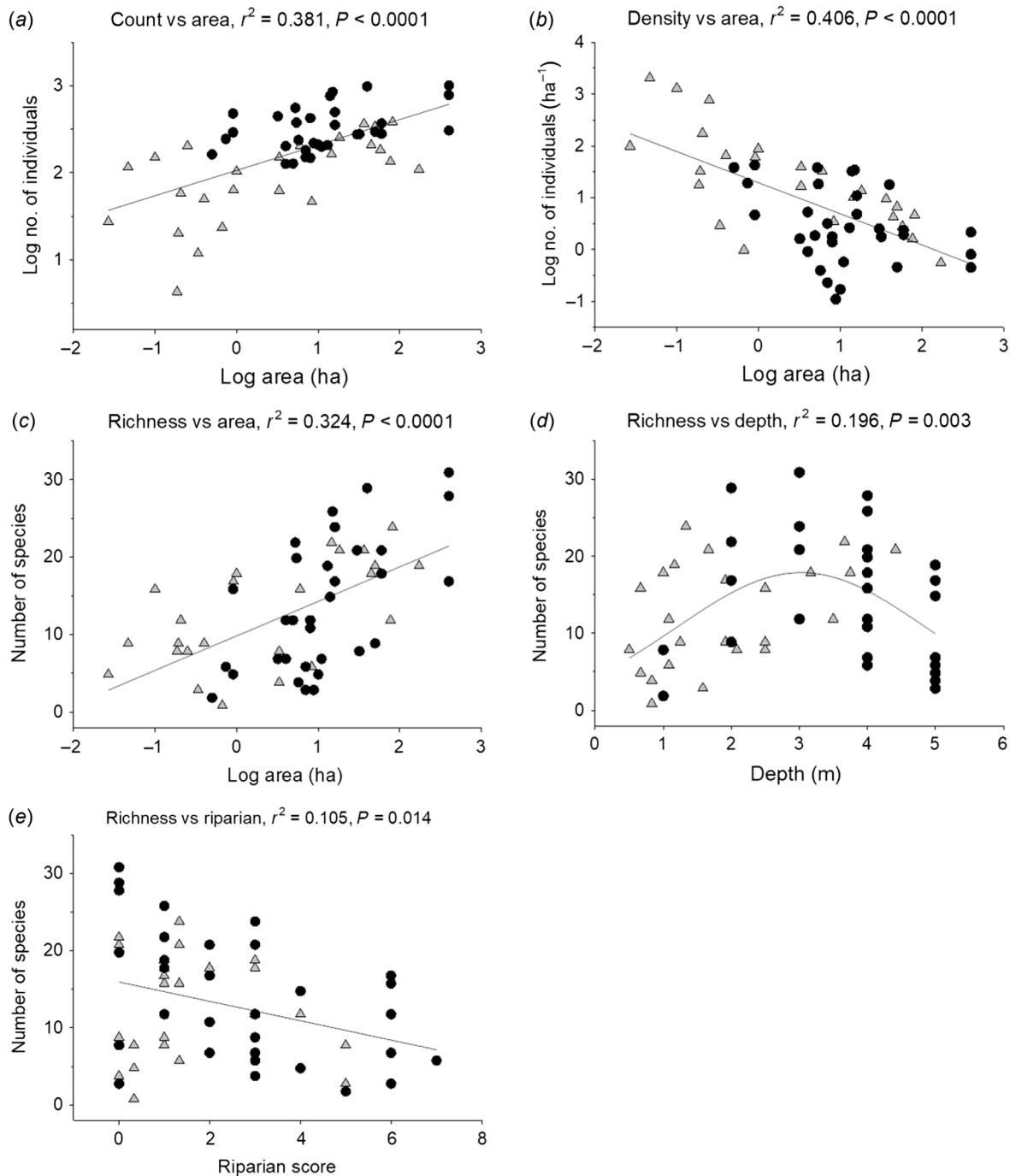


Fig. 2. Results of regression analyses of data from Surveys 1 and 2 to demonstrate relationships between: (a) waterbird abundance and wetland area; (b) waterbird density and wetland area; (c) waterbird species richness and wetland area; (d) waterbird species richness and wetland depth; and (e) waterbird species richness and wetland riparian integrity. Regression lines and associated r^2 values are indicated, based on linear models, except for peak model in (d). Symbols (some overlapping) represent all samples (sites and times: black circles, Survey 1; grey triangles, Survey 2).

$P = 0.098$), with antecedent annual rainfall (Pseudo- $F = 0.240$, $P = 0.875$) or flow (Pseudo- $F = 0.383$, $P = 0.840$); r^2 for the model = 0.052. Similarly, for presence/absence data, no relationship was evident for assemblages across years (Pseudo- $F = 1.687$, $P = 0.165$), with antecedent annual

rainfall (Pseudo- $F = 0.137$, $P = 0.933$) or flow (Pseudo- $F = 0.401$, $P = 0.788$); r^2 for the model = 0.059.

The NMDS of proportional abundance of species in assemblages over three decades also showed little evidence of temporal change but indicated, three distinct groupings

Table 2. Results of multiple regression analyses of bird species richness, total density and individual species' density versus environmental variables, of 15 species from Survey 1 for relationships where models have $r^2 > 0.25$ and $P < 0.05$.

Richness, total density and species identity	Predictor variables	t	P	Model F	Model P	Model r^2
Richness	Wetland area	4.04	0.0001	5.13	<0.0001	0.695
	Phosphate (PO ₄)	2.92	0.0047			
Total density	Sodium (Na)	−2.8	0.0066	1.96	0.0097	0.465
Little Egret	Phosphate (PO ₄)	6.05	<0.0001	20.3	<0.0001	0.900
	Total phosphorus (TP)	−3.02	0.0035			
	Dissolved oxygen (DO ₂)	2.46	0.0165			
	Conductivity	2.23	0.0291			
	Km from coast	2.07	0.0416			
Wandering Whistling-Duck	Ammonium (NH ₄)	4.47	<0.0001	5.5	<0.0001	0.710
	Phaeophytin	−4.11	0.0001			
	Total suspended solids (TSS)	2.93	0.0046			
	DO ₂	−2.75	0.0076			
	Nitrate + nitrite (NO _x)	2.34	0.0219			
	Magnesium (Mg)	2.11	0.0381			
Magpie Goose	Na	−3.7	0.0004	3.04	<0.0001	0.575
	Calcium (Ca)	2.67	0.0094			
	Discharge	−2.35	0.0218			
	NO _x	2.3	0.0246			
	Wetland area	2.14	0.0359			
Black-winged Stilt	PO ₄	4.69	<0.0001	2.99	0.0001	0.571
	TP	−4.71	<0.0001			
	Potassium (K)	2.6	0.0113			
	NH ₄	2.05	0.044			
	Km from coast	2.02	0.0471			
	NO _x	−2.01	0.0481			
Plumed Whistling-Duck	Chlorophyll <i>a</i>	3.21	0.002	2.74	0.0002	0.549
	K	−2.54	0.0132			
	Macrophytes	−2.23	0.0291			
	NH ₄	1.99	0.0502			
Masked Lapwing	Depth	−2.64	0.01	2.34	0.0015	0.510
	NH ₄	2.41	0.0186			
	Conductivity	−2.39	0.0195			
	K	2.3	0.0244			
	TP	−2.18	0.0328			

(Continued on next column)

Table 2. (Continued).

Richness, total density and species identity	Predictor variables	t	P	Model F	Model P	Model r^2
Yellow-billed Spoonbill	PO ₄	3.83	0.0003	2.24	0.0024	0.499
	Phaeophytin	−3.41	0.0011			
	NH ₄	3.23	0.0019			
	Depth	−2.58	0.0118			
	TSS	−2.1	0.0394			
Comb-crested Jacana	Na	−3.03	0.0034	2	0.008	0.470
	TSS	2.9	0.005			
	NH ₄	2.87	0.0053			
	PO ₄	2.34	0.0222			
	TN	−2.1	0.0395			
DO ₂	DO ₂	−1.99	0.0504			
Australasian Darter	Temperature	−2.93	0.0045	1.91	0.0119	0.460
	Wetland area	−2.22	0.0292			
	Drying	−2.17	0.0336			
Cattle Egret	TP	3.98	0.0002	1.83	0.0174	0.449
	Chlorophyll <i>a</i>	1.97	0.0521			
Australasian Grebe	Riparian	−2.82	0.0063	1.75	0.0256	0.438
	Wetland area	−2.64	0.0101			
	Na	−2.15	0.0352			
	Drying	−2.08	0.0409			
Australian Pelican	Conductivity	2.68	0.0091	1.71	0.0307	0.432
	Chlorophyll <i>a</i>	2.13	0.037			
Great Egret	Chlorophyll <i>a</i>	3.94	0.0002	1.68	0.0354	0.428
	NH ₄	3.43	0.001			
	K	−3.1	0.0028			
	Phaeophytin	−2.72	0.0082			
	Temperature	2.52	0.0138			
	TSS	−2.28	0.0256			
Intermediate Egret	Wetland area	−2.02	0.0472	1.64	0.0417	0.422
	Ca	3.28	0.0016			
	Mg	−2.19	0.0314			
Pacific Black Duck	Na	−2.73	0.0079	1.61	0.0476	0.418
	NH ₄	2.61	0.011			
	Mg	2.38	0.0201			

d.f. = 32, 72. Species ordered by r^2 . Explanation of the variables is provided in Table S6.

of surveys: at Wongaloo, Horseshoe Lagoon and the Burdekin-Townsville floodplain (Fig. 4a). ANOSIM demonstrated significance of the overall model (global $R = 0.772$, $P = 0.001$), and pairwise differences between all group pairs (Burdekin-Townsville floodplain (BT) and Horseshoe Lagoon (HL), $R = 0.940$, $P = 0.005$; BT and Wongaloo (W), $R = 0.68$, $P = 0.006$; HL and W, $R = 0.884$, $P = 0.001$).

Table 3. Results of DistLM analysis of the influence of environmental variables on bird densities in Survey 1 (with all samples – sites and times – combined in the similarity matrix).

Variable	d.f.	Pseudo-F	P	r ²	Cumulative r ² × 100%
Wetland area	103	6.596	0.001	6.02	6.02
PO ₄	102	4.583	0.001	4.04	10.06
Depth	101	3.801	0.002	3.26	13.32
Distance from sugarcane fields	100	3.804	0.002	3.18	16.5
Drying	99	3.887	0.001	3.15	19.65
Riparian species richness	98	2.600	0.007	2.08	21.73
Total (all 32 variables in model)	72				46.83

Only variables with $P < 0.05$ are shown.

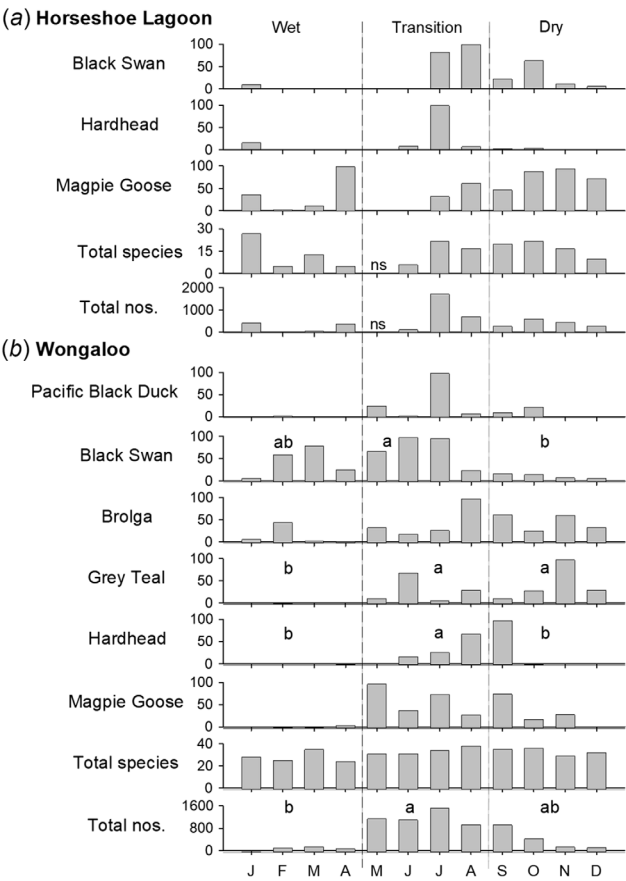


Fig. 3. Monthly relative abundance of common species (% of aggregated totals over 2015–2021), total abundance and total number of species over the same period at (a) Horseshoe Lagoon and (b) Wongaloo. Differences with $P < 0.05$ (Tukey test following repeated measures ANOVA) between Wet (January–April), Transition (May–August) and Dry (September–December) seasons (defined by vertical dashed lines) are indicated by letters a and b. Seasons were offset one month to the right for Hardhead analysis. ANOVA results are shown in Table S4. ‘ns’, no sample.

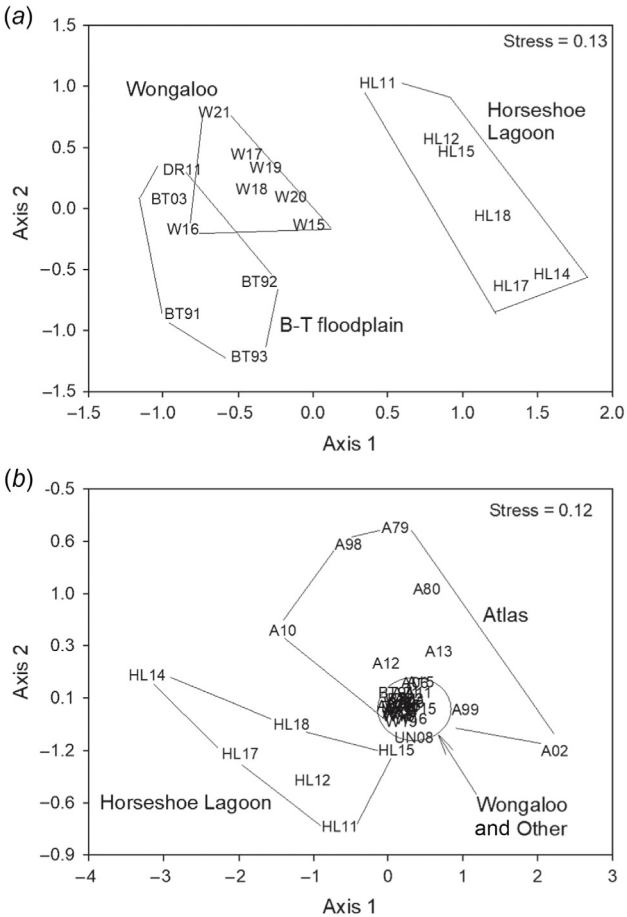


Fig. 4. Temporal distribution of annual data aggregated for identified samples, ordinated using multidimensional scaling plot of datasets: (a) over three decades (1991–2021) – proportional mean abundance (i.e. % composition) within a survey; and (b) over four decades (1979–2021) – presence/absence data. Samples are labelled by survey or site: A – BirdLife Atlas; HL – Horseshoe Lagoon (Atlas data); BT – Burdekin–Townsville floodplain (this study); W – Wongaloo (Atlas data); DR – Driscoll *et al.* (2012) ground surveys; UN – University of New South Wales aerial surveys; and by year (1979–2021).

In the NMDS of presence/absence data over four decades, again there was little evidence of temporal change, but two distinct groupings emerged: Horseshoe Lagoon and a combination of the three other groups (Atlas, Wongaloo and Other) (Fig. 4b). ANOSIM demonstrated non-significance of the overall model (global $R = 0.124$, $P = 0.143$), but pairwise comparisons found the Horseshoe Lagoon samples to be separate from those in Atlas and Wongaloo ($R = 0.530$, $P = 0.001$), and the ‘Other’ grouping, which included samples from the remaining surveys (global $R = 0.569$, $P = 0.002$). In these analyses, the Wongaloo site, which was not affected by intensive agriculture, notably grouped with Atlas and Other sites, some of which were subject to agricultural impacts.

Discussion

Hypothesis 1. Waterbird assemblages are generally similar among the wetlands surveyed

The Burdekin–Townsville freshwater wetlands provide extensive diverse habitats for a rich, and abundant waterbird fauna, estimated at 10 times the total waterbird abundance (excluding shorebirds) from the contiguous Bowling Green Bay Ramsar wetlands (Driscoll *et al.* 2012). In that study, four species occurred in internationally significant numbers (Cotton Pygmy Goose, Eastern Great Egret, Pacific Black Duck and Royal Spoonbill) and six further species in nationally significant numbers (Black Swan, Hardhead, Plumed Whistling Duck, Wandering Whistling-Duck, Intermediate Egret and Little Black Cormorant). The Ramsar wetlands support globally significant populations of shorebirds (Driscoll *et al.* 2012), some of which occurred in lower numbers in our study area. Our data correlate strongly with these and other records, despite differences in sampling design and extent, and the three- or four-decade span of the data. The most abundant species by numbers and biomass were vegetation feeders (Magpie Goose and Plumed Whistling-Duck) or generalist vegetation/invertebrate feeders (Pacific Black Duck) (Barker and Vestjens 1989; Garnett *et al.* 2015), which greatly exceed the biomass of specialist invertebrate feeders and piscivores, reflecting the expected trophic pattern of productivity. The populations of the grazers, Magpie Goose and Plumed Whistling-Duck, were likely boosted by the terrestrial food supply in well-watered grassland, including sugarcane headlands. Estimates of population size (Driscoll *et al.* 2012) produced one of the largest waterbird counts of eastern Australian wetlands when compared with 20 other important sites (Kingsford and Porter 2009).

Nestedness analysis found that individual assemblages were subsets of the entire set of samples, with no major habitat-based divisions. Nearly all species were represented in the larger wetlands, explaining the high level of nestedness. However, the inclusion of the Ramsar site would probably have shown a separation between the waterbird- and shorebird-dominated assemblages (Driscoll *et al.* 2012). Therefore, the broad requirements of many waterbird species are likely accommodated by the different wetland types, especially the larger ones, although some sites show distinct signatures in the ordinations. For example, samples from Horseshoe Lagoon were separated from the remaining samples, likely due to its perennial nature resulting from irrigation drainage.

Hypothesis 2. Wetland bird assemblages vary with wetland character

Abundance and species richness of waterbirds and functional groups increased with wetland area, as expected from the species richness/area relationship generally, and reflected by observations globally, such as in Tunisia (Hamza and

Selmi 2018), Amazonia (Cintra 2019) and China (Li *et al.* 2019). Sites with high species richness were large, with open water. Habitats included large, small, shallow, deep, permanent and temporary types, together providing most of the habitats required by the waterbirds. However, overall densities decreased with increasing area, as expected if the number of waterbirds was fixed. Additionally, the area of a particular habitat does not necessarily increase linearly with wetland size. Population size may also be limited by breeding success locally or further afield but this seems unlikely given the extent of the wetland/grassland complex for ground-nesting waterbirds and patchy woodland, gallery forest and extensive mangroves for those nesting in trees. Apart from the shorebird migrants, many of the common wetland species recorded are known or expected to breed within the wetland complex. The wetlands are also likely to provide a dry-season refuge for waterbirds whose breeding sites are elsewhere, as some of the seasonal data suggest. Waterbirds are likely to be subject to predation by native fauna and feral pigs but the impact is unknown.

The hump-shaped relationship of species richness with depth probably occurred because suitable habitat for many species was proportionately diminished in deeper waters. This was very clear for riverine lagoons that only had small areas of shallow water. Depth is a critical issue: for example, a global review indicates that a wide diversity of depths boosted diversity, with shorebirds restricted to less than 15 cm depth, dabbling ducks and large waders to about 25 cm and diving birds using much deeper waters (Ma *et al.* 2010). In the study area, dabbling ducks also occurred in deeper water in which submerged plants reached the surface. The Burdekin–Townsville complex provides large areas of shallow and deeper waters, thereby providing suitable feeding habitat for waders, dabblers and diving birds.

A negative relationship between bird species richness and riparian integrity was weak, possibly because (i) riparian condition declined with increasing area, as riparian vegetation was less well defined in the larger wetlands or (ii) waterbirds essentially prefer more open areas. Nevertheless, the local riparian vegetation and discrete woodland patches are important as breeding and roosting sites for several species. Total density, species richness and density of common species correlated with environmental variables (model $r^2 > 0.250$), including those relating to water quality, and especially indicators of productivity. There were no negative relationships with water quality, possibly because deep riverine lagoons, where weed infestation can cause poor water quality (Waltham *et al.* 2020), do not normally support many waterbirds. However, even deep lagoons can be attractive to Magpie Geese that feed on the invasive water hyacinth, and to predators such as Comb-crested Jacana and egrets that feed on animals found among hyacinth plants.

DistLM analysis of the assemblages explained ~47% of the variation in the data in a model that included all the environmental variables, each of which was very weakly associated

with the bird resemblance matrix, again indicating little evidence of strong reactions to human disturbance. Therefore, although agriculture, pollution and invasive species are implicated in the degradation of wetlands in southern Queensland (Bino *et al.* 2016), and in our study area the same is true for aquatic invertebrates and fish (Connolly *et al.* 2012; Pearson *et al.* 2019; Tibby *et al.* 2019; Waltham *et al.* 2020), the picture was less clear for the bird assemblages. Whether or not waterbirds are indirectly affected by such impacts is unknown. Water resource development has had a significant physical impact on the Burdekin–Townsville wetlands, as elsewhere (Kingsford and Porter 2009), yet substantial assemblages continued to use the wetlands.

The weak influence of anthropogenic factors on waterbird assemblages has been reported elsewhere (Daniel *et al.* 2021; Khaliq *et al.* 2019). In the Burdekin–Townsville area, the sheer extent and diversity of the mosaic of wetlands may absorb or buffer impacts and while this may not be true of highly modified wetlands such as Horseshoe Lagoon, even this wetland provided suitable habitat for many species. Additionally, waterbird assemblages may benefit from increased wetland habitat introduced by irrigation delivery and drainage channels, ponded pastures and artificial storages, possibly offsetting wetland loss due to land clearing and levelling, as may be the case for farm dams and rice fields (Hamilton *et al.* 2017; Herring *et al.* 2019). Nevertheless, active management is required for the whole ecosystem, including control of groundwater levels and salinity, with sea-level rise a developing threat in the region (GBRMPA 2019).

Hypothesis 2 was therefore largely supported with regard to morphology but, despite signals of the impacts of agriculture, the impacts were less substantial than expected for the bird assemblages. Cumulative impacts on waterbird assemblages may not yet be evident, although this is unlikely, given that three decades have passed since the major expansion of sugarcane cultivation (see below).

Hypothesis 3. Abundance and assemblage composition vary seasonally

A seasonal pattern was not clear at Horseshoe Lagoon, in which water levels were maintained by irrigation runoff. At Wongaloo, many common species varied seasonally in abundance and occurrence frequency, typically with a dry-season peak or no peak, except that migratory shorebirds mostly occurred during the wet season. Differences between years were inconsistent, indicating that no major trend or driver of change was operating. Our finding of reduction in abundance of some species during the wet season is likely due to local dispersal as habitats expanded or movement to different areas for breeding, as occurs in the Australian Northern Territory (Morton *et al.* 1990a, 1990b, 1993a, 1993b). We found that waterbirds subsequently returned to the wetlands for a great deal of the dry season, trailing off as wetlands dried and diminished in extent, in which case

there was a succession of waterbirds moving away, as expected. Seasonal movements were not as clear as in drier country (Halse *et al.* 2005; Kingsford *et al.* 2010), contrasting with the greater seasonality that is typical of inland Australia, where replenished habitat is exploited during and following the wet season (Kingsford *et al.* 2017; Caley *et al.* 2022) or following infrequent wet years (Halse *et al.* 2005).

Therefore our second hypothesis was supported, except that maximum abundances occurred after and not during the wet season.

Hypothesis 4. Assemblages vary among years according to antecedent rainfall

This hypothesis was not supported because there was little evidence that antecedent rainfall or flow were implicated in interannual variation among assemblages or individual species. As noted above, the Burdekin–Townsville wetlands are generally seasonal, although many are sustained through the dry season by normal or rising groundwater levels and irrigation tailwater that reduce interannual variability, in contrast with a large proportion of the continent.

Hypothesis 5. Assemblages have changed over several decades as a result of floodplain development

We summarised a substantial quantity of data but acknowledge that the different sources from different times may preclude substantiation of any conclusions. For this reason we were conservative in our approach and cautious in our interpretation. We found no evidence for bird assemblage change over the entire study period (three decades of proportional data, four decades of presence/absence data), despite the extensive agricultural development of the study area. Cumulative impacts were possibly not yet evident, except that it was approximately three decades since the major expansion of sugarcane growing. Undoubtedly, many wetlands were lost to or degraded by agricultural development (GBRMPA 2013; Davis *et al.* 2014; Waltham *et al.* 2020) but overall this loss appeared to be mitigated by the extent and diversity of remaining or novel wetlands, including modified and artificial wetlands as noted above. Using a rich dataset, Colloff *et al.* (2015) likewise demonstrated mixed trajectories or only minor decline in integrity of wetlands in the Murray–Darling area. We had limited data from before the expansion of intensive agriculture involving land clearing, levelling and irrigation development. However, the inter-decadal samples were collected in a similar timeframe to the agricultural development but no association was found. Additionally, some sites (e.g. Wongaloo and adjacent sites) were unaffected by agricultural development, providing control sites that corroborate our conclusion by grouping with our survey sites in multivariate analyses.

We should note that the bird assemblage data that we record are insufficient to track gradual trajectories in the

occurrence of rarer species, for which targeted surveys would be required. For example, the Australian Painted Snipe declined nationally during the study period with a recent Australian population estimate of only 340 (Rogers *et al.* 2021). Lavery and Seton (1974) recorded this species as 'uncommon' for our study area, while the Birddata database has only two records. Our broad surveys were inadequate to assess population size or change for this or other rare species.

Conclusion and conservation implications

The Burdekin–Townsville wetlands provide extensive, diverse habitats for a rich waterbird assemblage. Unlike many wetlands globally, the Burdekin–Townsville wetlands do not suffer a loss of water caused by irrigation agriculture (Lemly *et al.* 2000) as water is sourced from outside the system (the Burdekin River and Dam), and irrigation infrastructure (channels and storages) and tailwater supplement many wetlands (e.g. Horseshoe Lagoon and natural channels) either directly or through groundwater. Counts of six waterbird species (Black Swan, Hardhead, Plumed and Wandering Whistling-Ducks, Intermediate Egret and Little Black Cormorant) are nationally significant and total waterbird counts rank highly for eastern Australia, affirming the critical conservation importance of these wetlands (Kingsford and Porter 2009; Driscoll *et al.* 2012).

Despite data restrictions, the apparent absence of change in waterbird assemblages over three or four decades is noteworthy and indicates that the current extent and diversity of natural and artificial wetlands may provide a buffer against ecosystem impacts. If this is the case, they may similarly provide some protection against future changes such as those due to climate warming. Nevertheless, increasing salinity due to rising sea level in the Burdekin–Townsville coastal zone is likely to change wetland assemblages substantially with no upstream refuge available (Bernhardt 2022; Osland *et al.* 2022). Regular monitoring at a variety of sites, comparable to that undertaken at Wongaloo, is advisable to underpin appropriate water management, particularly for conservation goals. Additionally, special attention is required to identify and assess important breeding sites and mitigate threats to them.

Sica *et al.* (2020) suggested that conservation of many small rather than few large wetlands is preferable. Maintaining the full diversity of wetlands, from the smaller deep riverine lagoons to the expansive palustrine/lacustrine systems, would appear to be important for sustaining the full diversity of habitats through the seasons (Bühning-Gaese 1997) for the Burdekin–Townsville waterbirds. Ongoing management of the important ecosystem services and conservation values of the Burdekin–Townsville wetlands, the largest wetland complex on the Australian east coast, requires explicit acknowledgement of the importance and diversity of the wetlands (Adame *et al.*

2019). Although the nestedness analysis might suggest that management objectives could address environmental drivers and issues at a broad scale rather than piecemeal, the unique characteristics of each type of wetland and associated impact may warrant explicit individual conservation, as elsewhere (e.g. Murray *et al.* 2012). For example, deepwater confined lagoons, extensive multi-depth wetlands and small intermittent wetlands differ substantially with regard to weed and water-quality management (Waltham *et al.* 2020). Also, the nature of any potential special requirements of rare species is unclear.

Driscoll *et al.* (2012) found that ~90% of their waterbird data were recorded from outside the Ramsar site and therefore inadequate for protecting the palustrine wetlands, as elsewhere in Australia (Bino *et al.* 2016). Our results support this conclusion. Wetlands are treated as a continuum by waterbirds and other biota (Connolly *et al.* 2012; Tibby *et al.* 2019; Waltham *et al.* 2020; Pearson *et al.* 2021) and need to be recognised and managed accordingly. Although a great deal of focus has previously been placed on water quality (NQ Dry Tropics 2016) and the Ramsar site, it is gratifying to note that NQ Dry Tropics, the regional natural resources management body, is undertaking management activities across the wetland complex and catchment in keeping with management goals (NQ Dry Tropics 2016, 2024; Abbott *et al.* 2020). Likewise, the Great Barrier Reef Marine Park Authority supports coastal ecosystem protection, including areas of remnant floodplain set aside during the development of the BHWSS (GBRMPA 2013). In summary, the following are important conservation goals that will enhance not only bird assemblages but also aquatic biota:

- protecting remnant natural wetlands against future development;
- managing levels of groundwater and salinity of groundwater-dependent wetlands;
- water management to allow for natural seasonal flushing and drying;
- rehabilitation of watercourses and removal of barriers to allow natural connectivity between wetlands;
- identifying priority wetlands and undertaking rehabilitation as required;
- maintenance and restoration of riparian and contiguous terrestrial vegetation, especially to enhance waterbird breeding and roosting opportunities (Brandis *et al.* 2024);
- controlling pest species, especially invasive plants; and
- development of a floodplain management plan and monitoring program to integrate the needs of water use and ecosystem function.

Conservation management of the wetlands could benefit significantly from an overarching framework for regulation, on-ground management and dissemination of information to secure long-term health, given the national importance of these wetlands (Connolly *et al.* 2012; Driscoll *et al.* 2012),

as has been advocated for the whole Burdekin system (Pearson *et al.* 2022). Inclusion of a large proportion of the freshwater wetland complex in an expansion of the Ramsar site to the south would be a welcome development (Kingsford *et al.* 2021).

Supplementary material

Supplementary material is available online.

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

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